

Management and Conservation of Temperate Reef Fishes in the Grouper–Snapper Complex of the Southeastern United States

FELICIA C. COLEMAN¹ AND CHRISTOPHER C. KOENIG

*Institute for Fishery Resource Ecology, Department of Biological Science
Florida State University, Tallahassee, FL 32306-1100, USA*

ANNE-MARIE EKLUND

*National Marine Fisheries Service, Miami Laboratory, 75 Virginia Beach Drive
Miami, FL 33149, USA*

CHURCHILL B. GRIMES

*National Marine Fisheries Service, Tiburon Laboratory
3150 Paradise Drive, Tiburon, California, USA*

Abstract.—Effective fisheries management requires considerable information on life history characteristics, recruitment dynamics, habitat requirements, and fishery interactions for the managed species. It is clear that we have little of this information for any of the myriad temperate reef fishes managed in the South Atlantic or Gulf of Mexico regions, not only from our reliance on size limits, controlled effort, or limited harvest but from the repeated failures of all but complete closures of fisheries to allow recovery from overexploitation. Several of the life history features that reef fish share render them particularly vulnerable to both fishing pressure and habitat degradation, including their longevity, their slow maturation, their spatially and temporally predictable spawning aggregations, and the reliance of juveniles on estuarine nursery grounds. In addition, traditional hindcasting methods like virtual population analysis and the use of spawning-potential ratio to diagnose overfishing have not proved reliable means of assessing population status. Virtually unexplored in the United States to date are (1) use of marine fishery reserves to protect demographics and reproductive potential of exploited species, habitat and community structure of all species, and biodiversity and (2) use of forecasting methods of stock assessment based on juvenile abundances. We discuss the ability of these methods to provide insurance against management error and to predict fishery abundances for future year classes, respectively.

Marine fishes are regarded primarily as sources of food and sport, so they are extremely valuable economically. Marine fishery management should ensure that wild populations of these fish are sustained at commercially viable levels while meeting societal needs and the economic needs of fishermen. Because fish occur in variable environments, the harvest level must change in response to changes in abundance (Beddington and May 1977; Walters and Pearse 1996). In traditional management practice, however, life history is ignored, and each species' short-term economic value is protected to the complete exclusion of intrinsic, ecological, and even long-

term economic values. A belief persists that some combination of technological advances and harvest controls on individual species will produce sustainable fisheries, despite repeated management failures and fishery collapses, from Atlantic cod *Gadus morhua* in the North Atlantic (Martin 1995) to orange roughy *Hoplostethus atlanticus* in western Australia (Clark and Tracey 1993), Atlantic herring *Clupea harengus* in the North Sea, Peruvian anchoveta *Engraulis ringens* in Peru, and any number of reef fish species in the Caribbean (Sadovy and Eklund, in press).

In the southeastern United States (the Gulf of Mexico and the South Atlantic) the status of most reef fish stocks is unknown, including 60 out of 73 reef fish species in the South Atlantic

¹Corresponding author

and 50 out of 55 species in the Gulf (National Marine Fisheries Service 1997). Unfortunately, this lack of information is often interpreted as absence of a problem. In fact, all managed stocks of reef fish for which the status is known (13 in the South Atlantic, 5 in the Gulf) are either overfished or in danger of being so, with the exception of greater amberjack *Seriola drumeri*. Clearly, changes in fisheries management are needed that invoke a new ethic in fishing practices and incorporate effective conservation while maintaining the health and viability of marine ecosystems. More conservative, low-risk management practices are on the horizon (Walters and Pearse 1996), as witness the tremendous success of groups such as the Center for Marine Conservation in educating the broader public to fisheries crises.

Here, we first discuss the current status of reef fish fisheries in the southeastern United States, then show how the life history characteristics of dominant economically important species are related to declines in reef fish stocks, and finally make the case for a precautionary approach to management (Food and Agriculture Organization 1995) that protects stocks from overfishing through protection of essential fish habitat. Clearly, we must adopt a more farsighted response to the Magnuson-Stevens Fishery Conservation and Management Act (1996) if we are to combat the looming problems fisheries will face in the twenty-first century.

Current Status of Reef Fish Fisheries

The worldwide demand for fishes has increased dramatically in the last several decades, primarily because of overpopulation (Brown et al. 1995) but also because of per-capita increases in consumption (Hardin 1968; Holdren and Ehrlich 1974; Ehrlich 1994) and an increased ability to locate and capture fish through advances in fishing technology (Dayton et al. 1995). Members of the reef fish complex of warm-temperate and tropical regions appear to be particularly at risk. In the southeastern United States alone, for example, species currently either overfished or in danger of being so (National Marine Fisheries Service 1997) include red porgy *Pagrus pagrus*, black sea bass *Centropristis striata*, gag *Mycteroperca microlepis*, scamp *M. phenax*, snowy grouper *Epinephelus niveatus*, warsaw grouper *E. nigritus*, Nassau grouper *E. striatus*, speckled hind *E. drummondhayi*, jewfish *E. itajara*, red

snapper *Lutjanus campechanus*, vermilion snapper *Rhomboplites aurorubens*, white grunt *Haemulon plumieri*, and golden tilefish *Lopholatilus chamaeleonticeps*. Jewfish and Nassau grouper have been so heavily overfished that they are protected and are candidates for the endangered species list (Sadovy and Eklund, in press). Warsaw grouper and speckled hind may soon follow. The economic value of this species complex—1996 landings in the Gulf of Mexico of roughly 16 million pounds, an exvessel value near US\$36 million (Waters 1997)—makes protecting the sustainability of the fishery a critical consideration for this region.

Interaction of Life History Characteristics with Fishery Management

Many economically important reef fish species share a suite of life history characteristics that make them particularly susceptible to overexploitation. In addition, their behavioral characteristics exacerbate the problem—they show high site fidelity, regular migration among sites, complex social structure, and the ability to change sex. At least eight (about 73%) of the most overfished species are protogynous hermaphrodites. The combination explains why conventional management measures have entirely failed to stem commercial and recreational fishing pressure on this important group.

The large, economically important reef fishes tend to be long lived. Life spans range from about 25 to 40 years in warsaw grouper, jewfish (Manooch and Mason 1987; Bullock et al. 1992), and a number of snapper species (A. Johnson, National Marine Fisheries Service [NMFS] Panama City Laboratory, personal communication), to as high as 53 years in red snapper (Goodyear 1995). Even small species like damselfish *Stegastes altus* can live more than 15 years (Kohda 1996). Ages at maturity range from 3 to 5 years in gag (Johnson, personal communication) to 5–7 years in jewfish (Bullock et al. 1992) and red snapper (Goodyear 1995). The very low natural mortality rates in these large reef species (from 0.1 to 0.2 per year; Pauly 1980, 1997) imply that only a small portion of the biomass—perhaps as low as 10% (Walters and Pearse 1996)—can be sustainably harvested annually.

Fishing mortality rates are closer to 0.35–0.92 (30–60% annually), and fishing effort typically concentrates on the largest, oldest, most fecund individuals, which supply the bulk of the repro-

ductive output in any stock. The repeated result is a significant truncation in both the age and size structures of the population (Cuellar et al. 1996; Harris and McGovern 1997; Zhao et al. 1997; McGovern et al., 1998). In red snapper, for example, virtually the entire catch is of relatively small (35–45 cm), young (3–5 year old) individuals, many of which are just reaching sexual maturity (Goodyear 1995) in a species that can live up to 53 years and reach sizes of 90 cm. The negative effect on recruitment of loss of large females is obvious; one red snapper at 61 cm produces as many eggs as 212 red snapper at 42 cm (PDT 1990). Similarly, one gag at age 8 produces as many eggs as 48 gag at age 3 (Collins et al., 1998).

The largest, oldest individuals of some species are selectively removed from fished stocks both because they are the target of more intense fishing and because they frequent (at least seasonally) habitat that fishermen can locate with relative ease, such as high-relief reefs and shelf-edge outcrops (Man et al. 1995). Many species form consistent aggregations only during the spawning season (Domeier and Colin 1997), like Nassau grouper, gag, scamp, tiger grouper *M. tigris*, red hind *E. guttatus*, and jewfish (always containing the largest, oldest individuals in the population). Others, such as the deepwater yellowedge grouper *E. flavolimbatus*, snowy grouper, and warsaw grouper may also form ag-

gregations, but few data are available. This strong site fidelity—both to nonspawning habitat and to spawning sites to which they migrate annually—makes them vulnerable to fishers equipped with readily available electronic navigational and positioning equipment, with potentially devastating consequences.

Species with short spawning seasons that form a few large aggregations are more susceptible to severe overexploitation than are those with longer windows of opportunity for spawning in numerous smaller aggregations (Figure 1). Nassau grouper, for example, form large aggregations of up to 10,000 individuals (Smith 1972) in a few specific locations around the full moons of December and January (Colin 1992)—a total spawning window of roughly 10 d. Of the nearly 50 Caribbean aggregations known, at least 10 have been annihilated by fishing (Sadovy and Eklund, in press). Gag and scamp, by comparison, form smaller aggregations (<100 individuals; Gilmore and Jones 1992; Koenig, personal observation) distributed widely along the outer continental shelf (50–100 m depth) from the eastern Gulf of Mexico to North Carolina (Coleman et al. 1996; Y. Sadovy, Department of Ecology and Biodiversity, University of Hong Kong, personal communication). Gag spawning aggregations observed in the Atlantic in 1980 by Gilmore and Jones (1992) no longer exist at the same sites, as

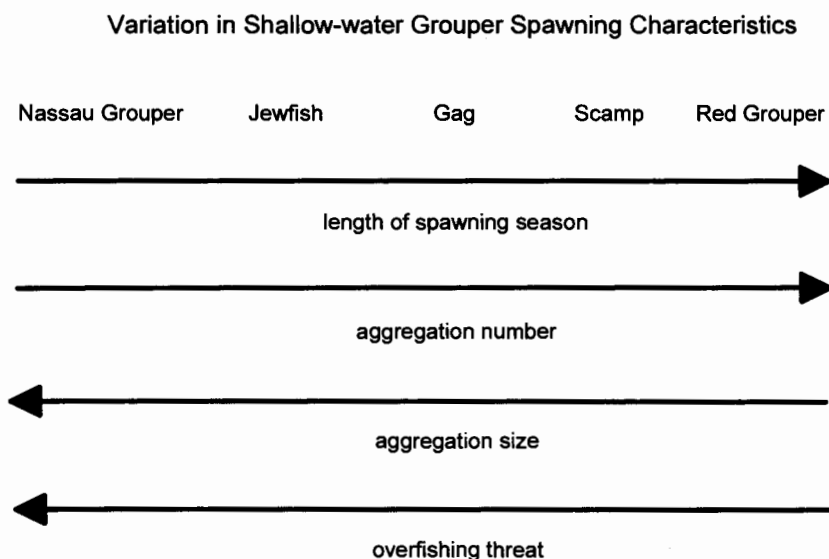


FIGURE 1.—Variation in shallow-water grouper spawning characteristics and relationship to the threat of overfishing. Arrows indicate increasing values for each characteristic.

a result of intense fishing pressure (Koenig et al., in press). Jewfish spawning aggregations, concentrated at depths ranging from 30 to 50 m along the southeast and southwest coasts of Florida, were heavily exploited from the 1960s through the 1980s by divers using powerhead-tipped spears. The population suffered such a dramatic decline that the fishery was closed in 1990 (Sadovy and Eklund, in press).

Studies on spawning-site fidelity in bluehead *Thalassoma bifasciatum* demonstrate that subsequent generations of fish must learn the locations of specific spawning sites (Warner 1990). When heavy fishing on aggregations removes the experienced fish, new recruits cannot find the aggregations, which can then collapse as functional spawning units. This appears to be what happened in orange roughy and Nassau grouper; aggregations were fished out and have not reformed (Clark and Tracey 1993; Sadovy and Eklund, in press). Aggregation fishing has also been implicated in the declining male:female sex ratios of gag and scamp in both the South Atlantic and the Gulf of Mexico (Coleman et al. 1996; Koenig et al. 1996). The percentage of male gag in the catch has fallen from about 17% in the late 1970s (Collins et al. 1987; Hood and Schlieder 1992) to 2–4% in the early 1990s; that of scamp from about 36% to 18% (Coleman et al. 1996). Although the significance of male loss is unknown, it is highly probable that such losses negatively affect reproductive success at the population level. The root cause of fishing-induced changes in sex ratio may be a disruption of the social structure of aggregations (Shapiro 1987), which alters the reproductive output of the spawning group if sex change is socially mediated. If sex change is size- or age-related, then fishing in this manner could be selecting against recovery by removing the age or size classes in which sex change occurs. In either case, no management plans currently in effect are designed to preserve the size, age, social structure, or the natural sex ratios or reef fish stocks.

Management of Reef Fishes

Often, each stage in the life history of a reef fish is associated with a different habitat and has very different recruitment dynamics (Gulland 1982; Frank and Leggett 1994). For example, all species of grouper and snapper spawn on offshore reefs, produce pelagic larvae that may disperse over hundreds of kilometers in the course of 20–

50 d and experience high density-independent mortality (Brothers et al. 1983; Jones 1991; Coleman et al. 1996). Larvae transported to nearshore nursery habitats settle as juveniles in seagrass beds, mangroves, oyster reefs, and marshes. Such species include gag, black grouper *Mycteroperca bonaci*, Nassau grouper, jewfish, black sea bass, gray snapper *Lutjanus griseus*, lane snapper *L. synagris*, hogfish *Lachnolaimus maximus*, white grunt, and to some extent red grouper *Epinephelus morio*. They move offshore after a nursery grow-out period and eventually recruit into adult populations. Although these characteristics make reef fishes, and especially gag, particularly tractable for description of recruitment processes, the same characteristics may make them largely unsuitable for management by traditional methods.

Reef Fish Stock Assessments

Management methods for reef fishes in the southeastern United States are based on catch-at-age data. The data are used in virtual population analysis (VPA) to reconstruct cohort-specific stock abundances and fishing mortality rates on the basis of past catches. The outcome of the VPA is then used to make annual recommendations for the total allowable catch (TAC). The greatest problem of VPA is that it provides only hindsight, information on cohorts that have passed through the fishery but none on the cohorts that need managing. Estimates of current cohort size based on historical trends impose a risk of underestimated fishing mortality, overestimated stock biomass, and misplaced optimism about the stock's condition (Walters and Hilborn 1992; Walters and Maguire 1996; Myers et al. 1997). Stocks can fall to dangerously low levels before management can identify and respond appropriately to the problem. The resulting drastic and reactive management actions have negative effects on the fishery species, the fishing industry, and the level of trust fishermen have in fisheries managers. The collapses of the North Atlantic cod and North Sea herring populations are cases in point (Walters and Hilborn 1992).

The predictive capability of recruitment forecasting allows management to anticipate problems and make preemptive adjustments to fishing pressure (de Lafontaine et al. 1992). Juvenile gag have proved an appropriate model for this approach because year-class strength is fairly easy to determine and relative recruitment success can be quantified (Koenig and Coleman

1998). Juveniles recruit as a single cohort over a short time period, remain in the seagrass nursery habitat throughout the summer, and egress as a cohort to nearshore reefs in fall (Keener et al. 1988; Ross and Moser 1995; Koenig and Coleman 1998). These characteristics have important implications for improving traditional assessments (based on fishery-dependent catch-at-age data) through fishery-independent surveys of juvenile abundance in forecasting models. The traditional VPAs could be tuned specifically in the year-classes of greatest interest to management (see, e.g., Myers et al. 1997). A limited time series on gag juvenile abundance, for example, when compared with catch-at-age structure of the population, suggests a strong correlation with fishery abundance as each of those year-classes recruits into the fishery (Johnson and Koenig, in press).

Spawning potential ratio (SPR), as it is traditionally determined, has also proved less effective for protogynous reef fishes than for the cold-temperate gonochorist fishes for which it was originally intended (e.g., Gabriel et al. 1989; Shelton and Morgan 1994). As defined by the Magnuson-Stevens Fishery Conservation and Management Act (1996), overfishing is "a rate or level of fishing mortality that jeopardizes the capacity of a fishery to produce the maximum sustainable yield (MSY) on a continuing basis." The emphasis in determining SPR has been and continues to be on the female's reproductive contribution, that is, egg production and the assumption that it is a valid measure of stock reproductive capacity. We know nothing about how male decline affects reproductive output, but it almost certainly does. The fallacy is in the assumption that egg production is equivalent to zygote production (Leviton and Petersen 1995). It behooves us, then, to examine the true range of possible effects for this group of fishes.

If the natural sex ratio in an unfished protogynous species is 5 females to 1 male and if, in a harem species, the natural sex ratio reflects natural harem size as determined over evolutionary time, then decline in males from 20% to 2% produces a sex ratio of 50:1 and could be equivalent to a 90% loss of male biomass. In such a case, either males must increase their harem size up to 10-fold to accommodate the new sex ratio or, if harem size does not increase, many females go unmated.

If harem size increases, each male has far greater reproductive potential than he would

have normally, but his fitness increases only if fertilization rates also remain high. If fertilization rate declines (see, e.g., Dewsbury 1982; Birkhead et al. 1995), then so does the reproductive success of the population. The second scenario also results in reduced reproductive success and recruitment overfishing.

Because current methods measure the decline in reproductive potential only as the numbers (= biomass) of males lost, they "see" only a loss of the largest size classes (the largest fish all being male), and SPR wrongly predicts a relatively small change in reproductive output, whereas a 90% decline in males could be equivalent to a 90% loss of reproductive potential. In reality, males probably can increase harem size somewhat without loss of fertilization success (Robert Warner, Department of Ecology, Evolution, and Marine Biology, University of California, personal communication), but this capacity is clearly not infinite. Because we don't know how elastic male reproductive capacity is, we must take a more conservative approach. The greater our uncertainty regarding a stock's reproductive capacity, the greater caution is needed in determining the effects of fishing on that stock. The SPR as typically determined for these fish is very unlikely to be a valid measure of the stock's reproductive capacity.

Traditional Management

Fishery management approaches typically consist of size and effort restrictions but do not often incorporate areal restrictions and are just beginning to consider the establishment of no-take areas. In Table 1, we present a simple matrix of those management measures and the life stages and ecological conditions potentially affected. We have given relatively optimistic assessments of the success of each strategy, although the components are unweighted as to their relative importance. In each case, we have considered the effects of a given strategy on protection of those life stages more susceptible to density-dependent processes—that is, juveniles, adults, and spawning adults rather than larvae. All strategies, with the exception of marine reserves, are based on single-species management practices.

Size limits.—Size limits are intended to exclude from the fishery immature fish (lower size limit), the fish that have greatest reproductive potential (upper size limit), or both (slot limit). Lower size limits supposedly ensure against

TABLE 1.—Management matrix of regulatory effort limitations for temperate reef fishes in the southeastern United States. Fisheries affected, R = recreational fishery, C = commercial fishery. + = positive management effect, 0 = no management effect.

	Size limit (RC)	Slot limit (RC)	Bag limit (R)	Trip limit (C)	ITQ (C)	Temporal restriction (RC)	Temporal spatial restriction (RC)	Spatial restriction (RC)
Single-species management								
Estuarine								
Juvenile stocks	0	0	+	+	+	0	0	+
Adult stocks	+	+	+	+	+	0	0	+
Shallow reefs (< 40 m)								
Late juvenile stocks	+	+	+	+	+	0	0	+
Adult stocks	0	+	+	+	+	0	0	+
Prespawning aggregations	0	0	0	0	0	+	+	+
Offshore reefs (> 40 m)								
Late juvenile stocks	0	0	+	+	+	0	0	+
Adult stocks	0	0	+	+	+	0	0	+
Spawning aggregations	0	0	0	0	0	+	+	+
Sex ratio	0	0	0	0	0	0	0	+
Ecosystem management								
Habitat	0	0	0	0	0	0	0	+
Genetic eiversity	0	0	0	0	0	0	0	+
Community structure	0	0	0	0	0	0	0	+
References to study fishing effects	0	0	0	0	0	0	0	+
Scores	2	3	6	6	6	2	2	13

growth overfishing because they are generally set at sizes that allow every individual at least one opportunity to reproduce. However, as depth of capture increases, so does release mortality (Rogers et al. 1986; Collins 1991; Parker 1991; Wilson and Burns 1996; Dixon and Huntsman, NMFS, Beaufort, North Carolina, unpublished). Because the vast majority of economically important reef species occur in a wide range of depths and stock declines cause fisheries to contract to areas of highest abundance, which are typically at greater depths, the effectiveness of size limits becomes questionable. Not only are the immature and first-year spawners unprotected, but the positive effects of a fortuitously large recruitment year can be significantly depressed by the high release mortality associated with a size limit. Such unreported discards were one of three dominant factors leading to the collapse of the Canadian cod fishery (Myers et al. 1997). The mortality of discarded fish not included in the catch-at-age data are unavailable to VPA.

Recent data indicate that undersize catch is high for many reef fishes in offshore waters of the Gulf of Mexico (Scott-Denton and Harper 1995; Johnson et al., in press). An exceptionally large gag year-class from 1993, in fact, dominated the 1996 catch both commercially (45% of total catch, 96% of undersize catch, and 31% of legal catch; Johnson et al., in press) and recreationally (53% of fish caught; Schirripa and Legault 1997). A high release mortality associated with a size limit can clearly have long-term negative effects on the stocks. Size limits are therefore most effective when restricted to hardy species that carry out their life cycles in relatively shallow water.

Effort Limitations.—Effort limitations, such as bag limits for recreational fishing and trip limits and individual transferable quotas (ITQs) for commercial fishing, effectively protect both juvenile and adult stocks (Table 1). A bag limit makes the fishery more inefficient but may do little to reduce fishing mortality if either the number of trips or the number of individuals fishing increases. Trip limits similarly restrict the allow-

able catch size per trip, but they are easily circumvented, and their potential benefits offset, by increases in days fished or trips taken (Huntsman and Vaughn, NMFS, Beaufort, North Carolina, personal communication). Although ITQs show some promise for eliminating these problems for the commercial fishery, the Magnuson-Stevens Act imposes a moratorium on their use as a management tool until the year 2000 (although in the southeast, ITQs are used in the wreckfish *Polyprion americanus* fishery).

Time and space closures.—Temporal and spatial-temporal restrictions typically imposed on a single-species basis prohibit fishing either during a particular time or for a short time over a particular area. They often simply shift effort to times outside the closed period, and they do not avoid the negative effects associated with discards.

Clearly none of these tools is well suited for reef fish, because of their ecological and behavioral characteristics (PDT 1990). Most effort limits operate as if the exploited species lived in isolation in space and time. In the absence of other changes in effort, the management strategy with the greatest promise is the use of marine reserves—spatially restricted absolute no-take zones—particularly when accompanied by reduced TAC to preclude effort shifts, but this is the least-often employed management tool in the United States. Besides the sanctuaries program in the Florida Keys, which is not a no-take program, only a single marine reserve exists in the entire southeastern United States—the Experimental Oculina Research Reserve (EORR) off the Atlantic coast of Florida. Even the EORR is not a true no-take reserve because it allows trolling for coastal pelagics, and its closure is for only a prescribed period of 10 years.

Besides protecting stocks, permanent spatial closures also protect physical habitat, age structure, perhaps genetic diversity of the stock, and community structure within the ecosystem. Agardy (1997) reviewed these aspects of marine fishery reserves extensively, so we address in detail only the issue of protecting essential fish habitat. This aspect of reserve use is important because even greatly reduced fishing mortalities cannot compensate for habitat degradation caused by harmful nonfishing and fishing practices (Pauly 1997). For many grouper species, essential habitats include estuarine nursery grounds, mid-shelf reefs, and outer-shelf reefs.

Reef fish in nearshore habitats have suffered

most from anthropogenous changes due to point and nonpoint sources of pollution and to structural alterations such as canalizations and water-diversion projects, which diminish or eliminate juvenile habitat. We need only look to coastal areas of Florida to see the effects. Seagrass beds in Tampa Bay, for example, have declined by about 80% since the 1960s; beds in Florida Bay have been so badly degraded that they may no longer be useful as nursery habitat (Butler et al. 1995). Although no estimates are available of the economic losses to fishery production associated with seagrass losses, quantitative estimates of potential fishery production clearly support adoption of protective measures.

Offshore reef habitats, particularly those important to demersal fishes, are susceptible to destruction by bottom trawl gear (Dayton et al. 1995; Pauly 1997), as has become particularly clear in our work in the EORR over the last few years. This shelf-edge reserve site was established in 1994 by the South Atlantic Fishery Management Council in large part to protect spawning aggregations of grouper. The reserve area was fished both before and after 1980, when Gilmore and Jones (1992) first documented significant spawning aggregations of gag and scamp. Since that time, however, hook-and-line fishing devastated resident grouper stocks (gag aggregations have been lost completely) while scallop dredge and trawl gear severely damaged the reef itself (Koenig et al., in press). Thus, in addition to the direct loss of fish populations, habitat and community structure are lost through the use of inappropriate gear.

Hampering our scientific understanding is a lack of controls. It is imperative that we gain those controls—and at the same time protect habitat integrity—by establishing marine reserves. No other alternative will let us examine the effects of fishing on exploited populations or examine marine ecosystem function. In addition, reserves provide an insurance policy for management. Every other manager, whether of a department store, a bank, or any other business, recognizes the value of insurance, yet we continue to put all our trust in the single basket of stock assessment, ignoring high variability in recruitment, ignoring high variability of environmental factors, ignoring the influence these factors have on our predictions of stock health, which as a consequence are tragically overoptimistic. Reserves provide significant insurance against recruitment variability, against habitat

destruction, against uncertainties in stock assessment, and most important, against our vast ignorance of ecosystem function.

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Edited by

John A. Musick
*Virginia Institute of Marine Science
College of William and Mary*

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